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LINKING ORGANISMAL FUNCTIONS, LIFE HISTORY STRATEGIES AND POPULATION PERFORMANCE

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Plant demographic and functional responses to management intensification: A long-term study in a Mediterranean rangeland

Eric Garnier[1] | Adeline Fayolle[1] | Marie-Laure Navas[2] | Christian Damgaard[3] | Pablo Cruz[4] | Daniel Hubert[5] | Jean Richarte[2] | Paul Autran[6] | Corentin Leurent[1] | Cyrille Violle[1]

[1]Centre d'Ecologie Fonctionnelle et Evolutive, CNRS – Université de Montpellier – Université Paul-Valéry Montpellier – EPHE, Montpellier Cedex 5, France; [2]Centre d'Ecologie Fonctionnelle et Evolutive, Montpellier SupAgro, CNRS – Université de Montpellier – Université Paul-Valéry Montpellier – EPHE, Montpellier Cedex 5, France; [3]Bioscience, Aarhus University, Silkeborg, Denmark; [4]INRA-AGIR, UMR 1248, Castanet Tolosan Cedex, France; [5]INRA-ERCC, UMR 868, Montpellier Cedex 1, France and [6]INRA, Unité expérimentale de La Fage, Roquefort sur Soulzon, France

Correspondence
Eric Garnier, Centre d'Ecologie Fonctionnelle et Evolutive, CNRS – Université de Montpellier – Université Paul-Valéry Montpellier – EPHE, 1919, Route de Mende, 34293 Montpellier Cedex 5, France.
Email: eric.garnier@cefe.cnrs.fr

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Abstract

1. Understanding how functional traits, which are key for plant functioning, relate to demographic parameters of populations is central to tackle pending issues in plant ecology such as the forecast of the fate of populations and communities in a changing world, the quantification of community assembly processes or the improvement of species distribution models. We addressed this question in the case of species from a Mediterranean rangeland of southern France.
2. Changes in species abundance in response to management intensification (fertilization and increased grazing pressure) were followed over a 28-year period. Probabilities of presence, and elasticities of the changes in the probability of space occupancy to colonization and survival, which are analogues of demographic parameters, were calculated for 53 species from the time series of abundance data using a space occupancy model. Nine quantitative traits pertaining to resource use, plant morphology, regeneration and phenology were measured on these species and related to demographic parameters.
3. The long-term dynamics of species in response to management intensification was associated with major changes in functional traits and strategies. Changes in the probability of occurrence—analogous to population growth rate—were correlated with traits describing the fast-slow continuum of leaf functioning. The elasticity of population growth rate to colonization was significantly related to reproductive plant height and seed mass, and to a lower extent, to leaf carbon isotopic ratio.
4. *Synthesis*. The functional response of species to management intensification corresponds to a shift along the second axis of a recently identified global spectrum of plant form and function, which maps, to some extent, onto the fast-slow continuum of life-history strategies. By contrast, the elasticity of colonization relates to the global spectrum axis capturing the size of organs. Seed mass contributes to this axis and is assumed to relate to one of the important traits structuring the

reproductive strategy axis of life histories as well, namely net reproductive rate. While this mapping between functional and life-history traits is appealing, further tests in contrasting types of communities are required to assess its degree of generality.

KEYWORDS
axes of functional variation, colonization and survival, fertilization, grazing, life-history strategy, plant population and community dynamics, plant traits, variations in species abundance

1 | INTRODUCTION

Changes in the composition of plant communities in response to changes in environmental conditions result from differences in recruitment and survival among species. A central tenet of trait-based ecology is that species with trait values conferring a higher probability to colonize and persist under particular local abiotic and biotic conditions are filtered in the community (Keddy, 1992; Woodward & Diament, 1991). Those particular traits that are associated with the response of plants to changes in environmental conditions ("response traits" sensu Lavorel & Garnier, 2002) should thus be related to modifications of demographic rates induced by these changes. However, a formal demonstration of the ability of plant traits to capture demographic changes, and ultimately, to be used as proxies for plant success in a given environment, remains to be done (Shipley et al., 2016). Such a demonstration is fundamental for many research areas in both functional and community ecology, including: (i) the forecast of the fate of populations and communities in a changing world; (ii) the quantification of community assembly processes through the lens of "modern coexistence theory" in which fitness and niche traits are dissociated; and (iii) the improvement of species distribution models and the parametrization of global vegetation models.

The search for relationships between plant traits and demographic parameters has yielded mixed results. In an early attempt, Silvertown, Franco, and McConway (1992) did not find any significant match between a demographic classification of species based on the contribution of growth, survival and fecundity to population growth rate, and the position of 18 herbaceous species in the Competitive–Stress-tolerant–Ruderal strategy scheme proposed by Grime (1979). This could be partly explained by the discrete quantification of ecological strategies—defined as a combination of traits that promotes growth and successful reproduction in a given environment (Craine, 2009; Grime, 1979)—potentially limiting the statistical power of the analysis. Functional ecology has moved towards a more continuous characterization of phenotypes through the use functional traits (Garnier, Navas, & Grigulis, 2016; Keddy, 1992; McGill, Enquist, Weiher, & Westoby, 2006; Violle et al., 2007; Westoby, Falster, Moles, Vesk, & Wright, 2002 for a synthesis), leading to the recent identification of a "global spectrum of plant form and function" ("global spectrum" hereafter; Díaz et al., 2016). This spectrum distributes species along two major axes: the first one organizes species according to their stature, organ size (leaf and seed) and stem specific density, while the second one describes the trade-off between resource acquisition and conservation at the leaf level ("fast-slow ecophysiological continuum" hereafter: cf. Reich, 2014; Wright et al., 2004). A number of empirical studies conducted in tropical forests have tried to quantify relationships between traits of the global spectrum and demographic parameters (Flores, Hérault, Delcamp, Garnier, & Gourlet-Fleury, 2014; Poorter et al., 2008; Visser et al., 2016; Wright et al., 2010). In these studies, stem specific density repeatedly appeared as significantly related to either growth or mortality, while relationships with other traits of the size axis (seed size, maximum height) were less consistent. Leaf traits were generally found to be only modestly informative of demographic processes (Poorter et al., 2008; Wright et al., 2010), except in the study by Flores et al. (2014).

In a search for broader generalizations, Adler et al. (2014) attempted to relate traits to vital rates (elasticities of the population growth rate to survival, growth and fecundity), based on the combination of world-wide databases of plant traits and demographic parameters. These authors found significant positive effects of seed mass on survival on the one hand, and positive relationships between both specific leaf area (the ratio of leaf area to leaf mass) and leaf nitrogen concentration (two traits involved in the fast-slow ecophysiological continuum) and fecundity on the other hand. One step further, Salguero-Gómez et al. (2016) recently proposed to identify the underlying components of plant life-history driving differences in vital rates among species. Based on the analysis of a world-wide dataset of nine features pertaining to gerenation time, individual longevity, growth and reproduction, these authors showed that life-history strategies could be characterized using two independent axes: a fast-slow continuum describing population growth and species longevity on the one hand ("fast-slow life-history continuum" hereafter, defined on completely different grounds from the fast-slow ecophysiological continuum described above), and a reproductive strategy axis, involving the net reproductive rate and the spread of reproduction across the life span of the individual, on the other hand. In a first analysis, Salguero-Gómez (2017) showed that specific leaf area, a major trait of the fast-slow *ecophysiological* continuum was, to some extent, related to the fast-slow *life-history* continuum, but not to the reproductive strategy axis.

With few exceptions (e.g. Flores et al., 2014), these studies did not take variations in environmental conditions into account and in the case of world-wide surveys, a single value for both traits and demographic parameters was assigned to each species. However, the idea that a trait value favourable in one environment may prove unfavourable in another one is at the core of the ecological strategy concept (Garnier et al., 2016 and references therein). This implies that the relationships between traits and demographic parameters will likely depend on the environment in which they are assessed. The objective of this study was precisely to investigate such relationships in the case of the response of rangeland species to an intensification of management practices, resulting from an increase in both fertilization and grazing pressure. To do so, we use a long-term experiment conducted in a Mediterranean rangeland of southern France. Vegetation censuses were performed yearly on permanent transects following intensification, offering prospects to assess analogues of demographic parameters using the method developed by Damgaard, Merlin, Mesléard, and Bonis (2011). It is expected that different functional traits play different roles in the life history of plants, and consequently affect the different demographic parameters in different ways. The relative importance of colonization and survival in determining observed changes in plant abundance is assessed by calculating the elasticities of population growth rate to these processes (Caswell, 2001). We specifically test the hypotheses that: (i) the combination of high fertility and high grazing select species from the fast end of the fast-slow ecophysiological continuum; these two environmental factors generally have opposite effects on size-related traits (plant height, leaf area, seed mass), making predictions for these traits delicate (see Garnier et al., 2016 for a synthesis of these different effects); (ii) the selection for short-lived species with a high population growth rate that produce numerous well-dispersed offspring (cf. Schippers, van Groenendael, Vleeshouwers, & Hunt, 2001 and references therein) is expected under high grazing intensity, but this will likely depend on how demographic parameters respond to the concomitant increase in fertility (i.e. grazing × fertility interaction); and (iii) the traits that capture the two major axes of functional variations of the global spectrum relate to population growth rate on the one hand, and to the elasticities of population growth rate to colonization and survival on the other hand. We first analyse the long-term changes in community composition and the dynamics of species sorting. We then characterize the response of each species individually and classify them into three response groups (i.e. species which respond in similar ways to specific environmental factors: Lavorel, McIntyre, Landsberg, & Forbes, 1997) based on their demographic response to intensified management. Using nine traits capturing plant form and function, we then test the degree of association between the demographic and functional responses, and discuss how the latter can be mapped to key features structuring species life history.

2 | MATERIALS AND METHODS

2.1 | Study area

The study site is located on the "Causse du Larzac", a limestone plateau located in the Mediterranean region of Southern France which is exposed to recurrent summer droughts and severe winter conditions. Mean temperature of the coldest and warmest month are respectively 1 and 19°C, and rainfall oscillates between 680 and 1,790 mm with a mean of 1,074 mm (onsite records over the period 1973–2005). During the severe European heatwave in 2003, the field site experienced the lowest summer precipitation and temperature over the period 1973–2005.

2.2 | Overview of the experiment

A long-term experiment of intensified management was conducted on the rangelands of the INRA "La Fage" experimental station (43°55′N, 3°06′E, 765–830 m a.s.l.), to increase the spring offer of biomass available for sheep (Molénat et al., 2005). Two experimental paddocks of 6.5 ha each were fertilized with nitrogen (60 kg/ha each year, half of them in spring and the other half in autumn) and phosphorus (40 kg/ha during spring every 3 years) over the 1978–2005 period ("G+F" regime hereafter). In these G+F paddocks, increased fertilization was accompanied by an increase in the intensity of disturbance: the proportion of biomass removed annually by grazing relative to the total biomass produced increased from 0.20 kg/kg (which corresponds to a stocking rate of *c*. 1 sheep/ha) to 0.61 kg/kg, with the establishment of intense grazing in spring during the peak of biomass production. The intensification of management therefore corresponds to a combination of increased fertility and grazing. To assess the effects of this intensification, which was applied to 6% of the farm area, vegetation dynamics in G+F was compared to that of unfertilized paddocks maintained under traditional management practices (low grazing maintained at 0.20 kg/kg: "GU" regime hereafter), which thus constitutes a control against which the intensified regime can be compared.

2.3 | Botanical censuses and demography of space occupancy

In G+F, botanical censuses were conducted yearly during the experiment at peak standing biomass (usually in May) on 16 permanent transects. In GU, censuses were conducted in 1981, 1986, 1995, 1999 and 2004 on 16 transects. Each transect was 5 m long, and all species in contact with a vertical pin placed every 10 cm (50 pin-points *per* transect) were recorded. A total of 154 plant species was recorded in the floristic dataset. Botanical synonyms were standardized using the TaxRef (version10) taxonomic referential (https://inpn.mnhn.fr/telechargement/referentielEspece/referentielTaxo). Species abundance was calculated as the total number of occurrences per transect per year (i.e. species cover).

We characterized the long-term response of 53 species to intensified management from the yearly censuses available in the G+F, using the analogues of demographic parameters derived from the space occupancy model developed by Damgaard et al. (2011), detailed in Appendix S1. Briefly, changes in probabilities of occurrences (π, analogue to population growth rate), and the relative importance of the two demographic processes, colonization

and survival, in determining the observed cover changes were assessed by the elasticities of colonization ($Elast_c$) and survival ($Elast_s$: see equations A2 and A3 of Appendix S1). These elasticities were calculated for each species from the pin-point time-series data, and the relative importance of the two elasticities for population growth rate were calculated as $Elast_{c\ or\ s}/(Elast_c + Elast_s)$. Since these values sum up to one (cf. Table S1), we present only results for colonization on figures. The terms colonization and survival are used here for the two events that a new species is observed at a specific position, and the same species is observed at the same position as in the previous year respectively. However, the positions of the pin-point might vary slightly from year to year, which may sometimes lead to biases in the assessments of colonization or mortality events (discussed in Damgaard et al., 2011; Damgaard, Merlin, & Bonis, 2017).

2.4 | Plant traits

In 2006 and 2007, we measured nine traits on the 53 species for which it was possible to calculate proxies for demographic parameters (Table S1), following standardized protocols (Pérez-Harguindeguy et al., 2013). The traits of species observed in the initial state of the community but no longer present in paddocks of the G+F management regime at the time of trait measurements were measured in the GU paddocks. We checked that there was only little interannual variation in the trait values on a set of 13 species (Fayolle, 2008). The significance of the traits for the functioning of organisms, briefly summarized below, is further detailed in Pérez-Harguindeguy et al. (2013) and Garnier et al. (2016), while terminology follows Garnier et al. (2017). These are given below.

2.4.1 | Plant stature and reproductive traits

Reproductive plant height (RPH), taken as an indicator of overall plant stature and of seed releasing height, was measured on 30 individuals per species. Weekly censuses over the growing season enabled us to accurately determine the onset of flowering (OFL), taken as an indication of the timing of resource use during the course of the growing season. To account for temperature differences between the 2 years of measurement, OFL was expressed in growing degree day using a base temperature of 5°C (cf. Bonhomme, 2000). Finally, seed mass (SM) which affects many aspect of the ecology of plant regeneration, was measured on five samples containing 10–50 seeds depending on species reproductive outputs and collected on at least 10 individuals.

2.4.2 | Leaf traits

Three leaf morphological traits were measured: leaf area (LA) which relates to a number of processes including energy and water exchanges between the leaf and the atmosphere; specific leaf area (SLA, the ratio between leaf area and leaf dry mass) and leaf dry matter content (LDMC, the ratio between leaf dry mass and leaf fresh mass), which correspond respectively to the area deployed *per* unit mass of a leaf (scales positively with photosynthetic rate and negatively with leaf life span) and to leaf tissue density. These three traits were measured on fully rehydrated leaves collected on 10 individuals per species.

In addition, three traits relative to the chemical composition of leaves were assessed: mass-based leaf nitrogen content (LNC) which relates to protein content (especially Rubisco) in the leaf, and mass-based leaf phosphorus content (LPC), reflecting the content per unit mass of nucleic acids, lipid membranes and bioenergetic molecules such as ATP, providing information on leaf metabolic machinery. Finally, leaf carbon isotopic discrimination ($L\delta^{13}C$) was used as a proxy for water use efficiency. LNC, LPC and $L\delta^{13}C$ were measured on four (three for $L\delta^{13}C$) samples obtained by pooling and grinding the 10 leaves used for SLA and LDMC measurements.

As species from different life cycles (annuals vs. perennials) and life-forms (sensu Raunkiaer, 1934) have been shown to have contrasting demographic characteristics (Silvertown, Franco, Pisanty, & Mendoza, 1993; Stott, Franco, Carslake, Townley, & Hodgson, 2010) and are likely to respond differently to changes in environmental factors induced by the intensification of management (cf. Grime, 1979), these information were collected for the 53 species listed in Table S1 from a local flora (Bernard, 2008).

2.5 | Data analyses

To assess the impact of management intensification on vegetation, the long-term changes and differences in species composition between the intensified and traditional regimes were quantified using the Sørensen similarity index (cf. Jost, Chao, & Chazdon, 2011) using the 5 years when botanical censuses were available in the two regimes. This index, which is incidence-based and does not take species abundances into account, was calculated over time and space in three different ways: (i) over time within each of the two management regimes, by comparing the species composition of each of the 16 transects in 1986, 1995, 1999 and 2004, to that of the initial censuses conducted in 1981 taken as a reference (Figure 1a); (ii) for each of these 5 years, by comparing (ii_a) the value of the index for the 16 transects within each management regime and (ii_b) the average value of the index between the two regimes. This second set of calculations allows us to quantify the divergence in species composition resulting from the intensification of management. The Sørensen index varies from 1 for communities of similar species composition to 0 for communities which do not have any species in common. Calculations were done using the EstimateS software (Colwell, 2013). The temporal trend of the index was tested using linear regressions, while differences within and between the two management regimes were tested using two-way (transect and year) ANOVAs followed by post hoc Tukey tests.

Species were classified into three response groups according to their response to management intensification in the G+F regime (cf. McIntyre & Lavorel, 2001; Noy-Meir, Gutman, & Kaplan, 1989): "decreasers," for which π (change in the probability of occurrence) has a value lower than 0.99; increasers, which have a π value higher than

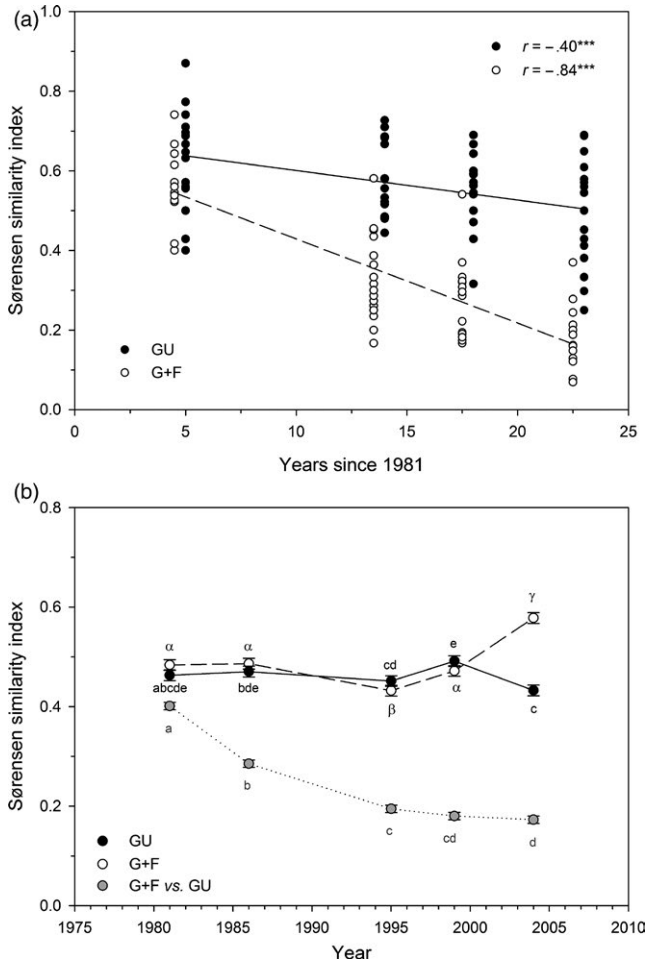

FIGURE 1 Sørensen similarity index calculated for the 5 years when botanical censuses were conducted in both the traditional (GU) and intensified (G+F) management regimes. In (a), changes with time in the index values calculated for each regime are shown. Each point represents a transect along which botanical censuses were conducted (16 points for each management regime and year); correlation coefficients (*r*) of the two linear regressions are given at the top of the panel (slopes are significantly different between the two regimes). In (b), the back (solid line) and white (dashed line) points represent the average values of the index (with error bars) calculated for the 16 transects of the traditional and intensified management respectively; the grey points (dotted line) represent the average value of the index calculated between the two management regimes; different letters show a significant year effect (tested with two-way ANOVAs followed by post hoc Tukey tests) on the value of the index: Latin and Greek black letters compare values within the traditional and intensified regimes respectively; grey letters compare values calculated between the two regimes

1.01; and "stable species" which have a π value comprised between 0.99 and 1.01. To assess the sensitivity of results to this procedure, we also ran the analyses in two other ways: (i) we set thresholds π values of 0.90 and 1.10 to define the three groups of species, and (ii) we took a continuous rather than a discrete approach, and tested relationships between traits and population growth rates without classifying species into groups based on their π value. Results derived from these two procedures are qualitatively similar to those found using the 0.99–1.01 threshold values, and are presented in the Supplementary Information.

Differences in trait values between the three groups were then tested (i) on a trait by trait basis, (ii) on trait combinations derived from a principal component analysis (PCA) conducted on the species (n = 53) × traits (n = 9) matrix, using the coordinates of species on the two first components of the PCA for which eigenvalues were greater than 1.0, making possible the comparison with Díaz et al. (2016) analysis. The three size-related traits (reproductive height, seed mass and leaf area) were log transformed prior to these analyses, to fulfil normality assumptions. The significance of differences between groups was then assessed using one-way ANOVAs followed by post hoc Tukey tests. The relationships between traits and the elasticities of population growth rate to colonization and survival were tested using linear regressions. This was done for each trait on the one hand, and using the coordinates of species on the first two axes of the PCA described above on the other hand.

Unless otherwise stated, all statistical analyses were performed within the R environment (R Development Core Team, 2016).

3 | RESULTS

3.1 | Community dynamics

The long-term experiment of intensified management induced strong changes in biomass produced and species composition. In particular, the 28-year period of intensification led to a 2.7-fold increase in maximum above-ground standing biomass in spring (Chollet et al., 2014). Changes in species composition can be summarized by comparing the temporal trajectory of the Sørensen similarity index in the two management regimes: while the values of the index significantly decrease with time in both regimes (Figure 1a), the slope of the relationship is significantly steeper (F = 24.5, p < 0.001) in G+F than in GU, indicating a faster rate of species replacement in G+F. These temporal changes appear to be relatively homogeneous within each of the two regimes, as shown by the stability of Sørensen index values calculated for a given year in each of the G+F and GU regimes (white and black symbols on Figure 1b respectively); by contrast, the species composition progressively diverged with time between the two regimes (grey symbols on Figure 1b). The strong turnover observed in 2005 in G+F (Figure 1b) might be related to the severe 2003 summer drought, whose effect appears to have been much less pronounced in GU.

The temporal changes induced by management intensification in G+F correspond not only to species replacement as assessed by the Sørensen index but also to changes in abundance of both dominant and less abundant species, as shown in Figure 2 for the 53 species for which demographic data are available. Species composition shifted from a quasi-dominance of *Bromopsis erecta* and the presence of several perennial grasses and graminoid species at lower abundance, such as *Festuca christiani-bernardii*, *Carex humilis* and *Brachypodium*

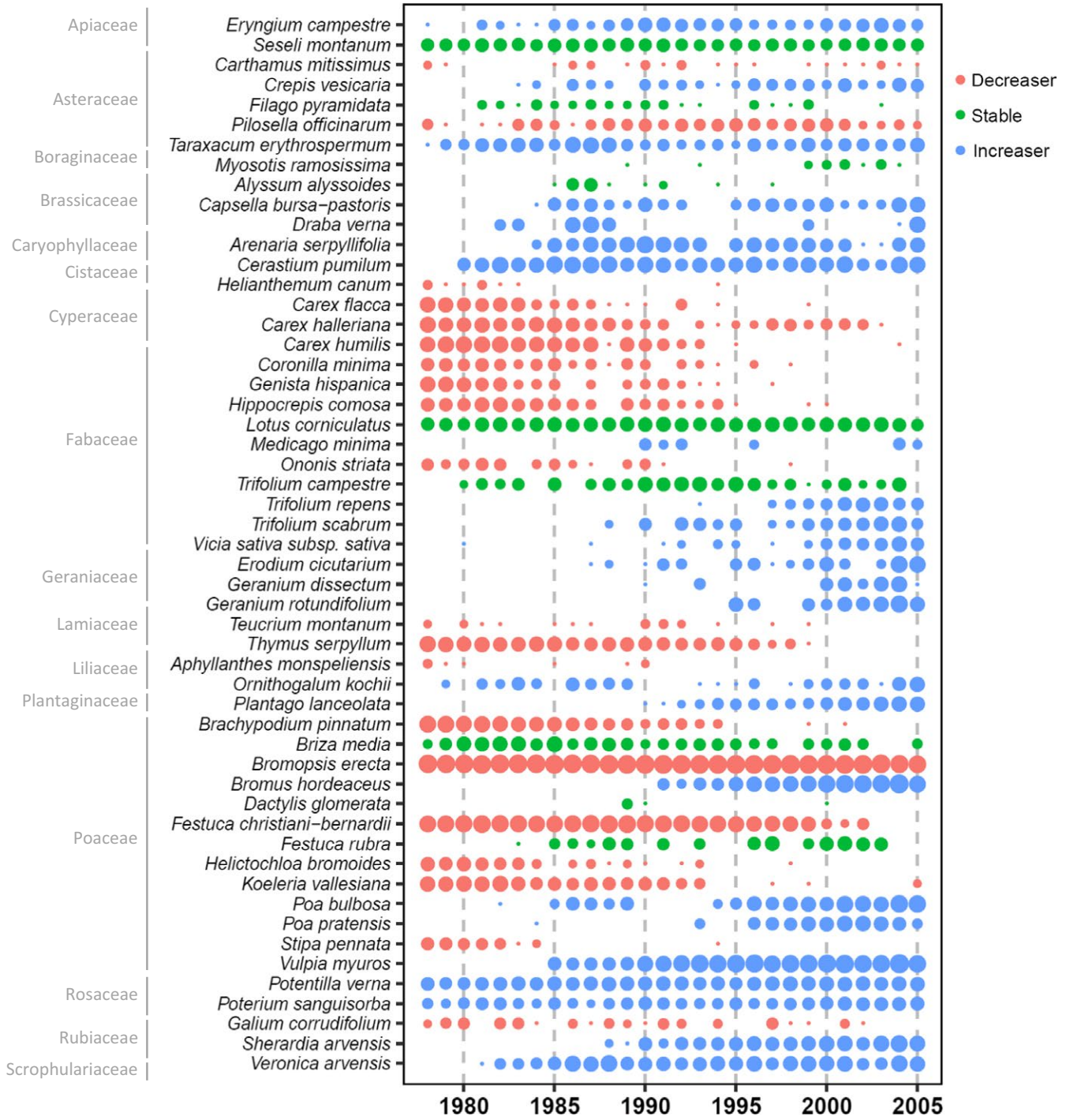

FIGURE 2 Temporal variations in the abundances of the 53 examined species for which analogues of demographic parameters are available (listed in Table S1), as measured in the intensified management regime (G+F) from 1978 to 2005. The size of the dots is proportional to the absolute abundance of species, calculated each year for the 16 transects. Colours correspond to the three response groups: decreasers (red), increasers (blue) and stable species (green) [Colour figure can be viewed at wileyonlinelibrary.com]

pinnatum, to an increase in occurrence of annual species (e.g. *Vulpia myuros*, *Bromus hordeaceus* for grasses, *Sherardia arvensis*, *Geranium rotundifolium* for forbs) and also short-lived perennials (*Poa bulbosa*). Long-term changes in abundance patterns were monotonic for some species (e.g. *Carex halleriana*, *Vulpia myuros*), but intervals of rapid change followed by relatively stable periods can also be identified for some of the species (e.g. *Arenaria serpyllifolia*, *Trifolium campestre*), as well as alternations of periods when species are present in or absent from the community (e.g. *Carthamus mitissimus*, *Galium corrudifolium*).

3.2 | Demography, response groups and plant traits

Among the 53 species for which analogues of demographic parameters could be assessed in G+F using the temporal changes of species

cover, 20 are categorized as "decreasers," 24 as "increasers" and 9 as "stable" (Figure 2, Table S1). The elasticity of population growth rate to colonization varied between 0.29 and 0.99, while the elasticity of survival varied between 0.01 and 0.52 (Table S1). The elasticities of colonization and survival were positively and negatively related to changes in the probability of occurrence respectively, but these relationships were not significant.

The π values of annuals varied from 1 (stable population) to 1.54 (population increased by 54% over the 1978–2005 period), while those of perennials varied from 0.67 (population decreased by 33% over the 1978–2005 period) to 1.42 (42% increase: Table S1 for individual values). The average values for these two groups were significantly different (Figure 3a): annuals were mostly increasers (14 species out of 18), while perennials were decreasers (20 species: all species in this group), increasers (10 species) or stable (5 species). Among perennials, chamaephytes had slightly, but not significantly, lower average π values than herbaceous perennials (hemicryptophytes + geophytes: Figure 3b); all chamaephytes were decreasers (Table S1). The elasticities of population growth rate to colonization were also significantly higher in annuals than in perennials (Figure 3c), but the difference was larger for herbaceous than for woody perennials (Figure 3d). Symmetric results were found for the elasticity of survival (data not shown).

Five traits were found to differ significantly between species of at least two of the three response groups: SLA, LPC, OFL, LDMC and $\delta^{13}C$ (Figure 4i,k,m,o,q). Among these, only LPC and LDMC differed significantly between increasers and decreasers (Figure 4k,o). For the three other traits, there were significant differences between stable species and at least one of the two other groups (Figure 4i,m,q). None of the other five traits measured differed significantly among the three groups (Figure 4). Using the 0.90–1.10 threshold values for π (instead of the 0.99–1.01 values: cf. Section 2) had a very limited impact on the results (compare Figure 4 with Figure S1). When a continuous rather than a discrete approach was used (see Section 2), significant relationships between traits and population growth rate were found for LPC and LDMC (Figure S2). Relationships were not significant for the other traits; for the three traits which differed between stable species and one of the two other groups (SLA, OFL and $\delta^{13}C$), nonlinear (nonsignificant) relationships between trait values and π were found (Figure S2i,m,q).

The first component of the PCA run on the nine traits is strongly structured by the leaf traits that discriminate species on the basis of their response to intensification (Figure S3 and Table 1 for loadings): as a consequence, the average score of decreasers on this component differed significantly from that of the two other response groups (Figure 5a and Figure S4). The second component of the PCA was mainly driven by size-related traits (RPH, leaf area) and seed mass, and to a lower extent by leaf $\delta^{13}C$ (Table 1, Figure S3. There was no significant difference between

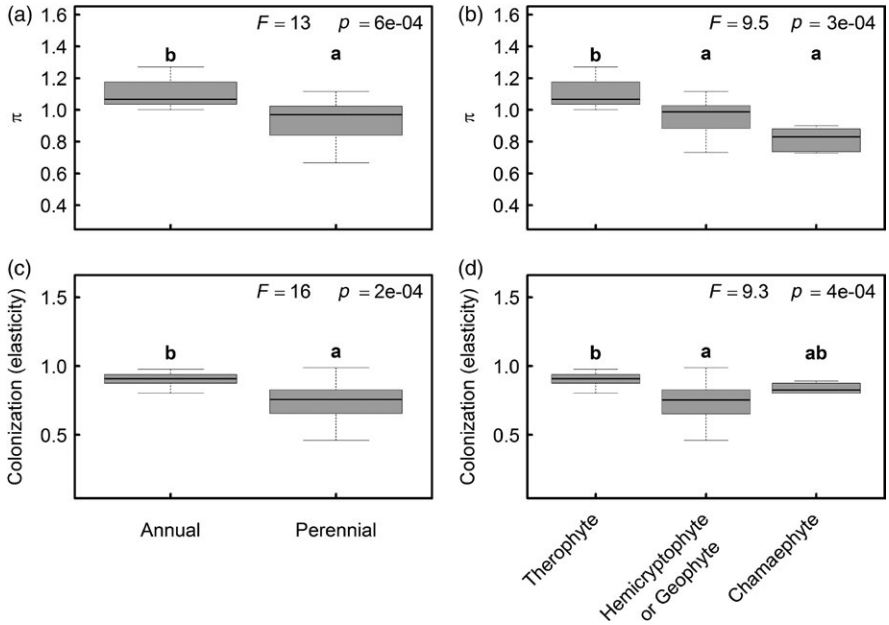

FIGURE 3 Distributions of changes in the probability of occurrences (π: a and b) and elasticities of colonization (c and d) for annual and perennial species (a and c), and species from different Raunkiaer life-forms (b and d), calculated in the intensified management regime (G+F). Box plots characterize this distribution, with the bottom and top part of the box indicating the 25th and 75th percentile, respectively, the two whiskers the 10th and the 90th percentile, respectively, and the horizontal line within the box the median value. The *F* value of analyses of variance testing for differences between groups and the significance level of these differences (*p* values) are given at the top of each panel; different letters above the box plots indicate significant differences between groups. Since there was only one geophyte in our dataset (*Ornithogalum kochii*: cf. Table S1), hemicryptophytes and geophytes were merged into a single group corresponding to "herbaceous perennials"

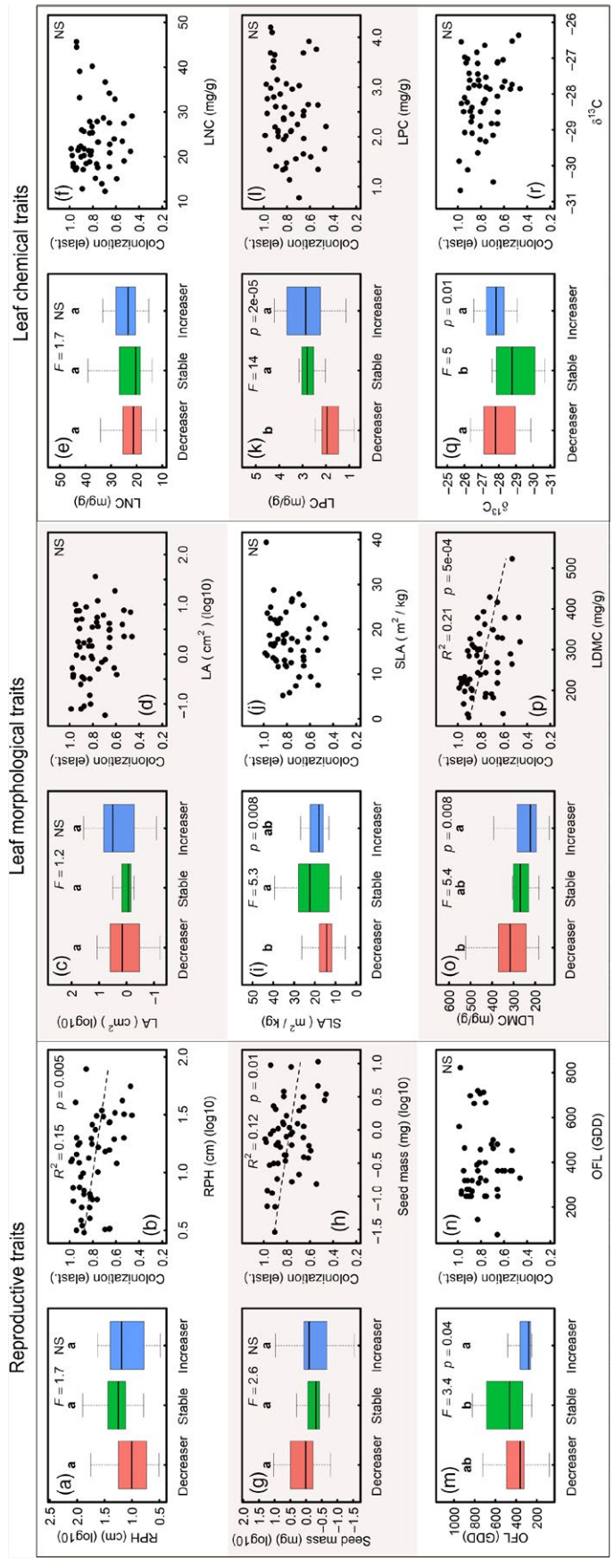

FIGURE 4 Distributions of trait values of species from the three response groups (increasers, decreasers and stable species) shown as boxplots, and relationships between traits and the elasticity of population growth rate to colonization, calculated in the intensified management regime (G+F). On panels a, c, e, g, i, k, m, o and q, response groups are identified on the basis of the values of changes in the probability of occurrence; more information on boxplots and meaning of letters and text can be found in the legend to Figure 3. On panels b, d, f, h, j, l, n, p and r, the coefficient of determination (R^2) and the significance (p value) of linear regressions between the two variables is given on top of the panel (NS: not significant); dashed lines indicate significant relationships. Colour code for all panels: red, decreasers; blue, increasers; green, stable species. The nine traits are: RPH: reproductive plant height (a and b); Seed mass (g and h); OFL: onset of flowering, expressed in growing degree day (m and n); LA: Leaf area (c and d); SLA: specific leaf area (i and j); LDMC: leaf dry matter content (o and p); LNC: leaf nitrogen concentration (e and f); LPC: leaf phosphorus concentration (k and l); $\delta^{13}C$: leaf carbon isotopic ratio (q and r) [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 1 Percentage of explained inertia (% inertia) by the first two components of the principal component analysis (PCA), and loadings of traits on these components. The PCA was run using the nine following traits: reproductive plant height (RPH), seed mass, onset of flowering (OFL, expressed in growing degree days), area of an individual leaf (leaf area), specific leaf area (SLA), leaf dry matter content (LDMC), leaf nitrogen concentration (LNC), leaf phosphorus concentration (LPC) and leaf carbon isotopic ratio (Lδ^{13}C)

	Component 1	Component 2
% inertia	28.2	21.2
RPH ($\log_{10}$)	−0.255	−0.637
Seed mass ($\log_{10}$)	−0.082	−0.656
OFL	−0.231	−0.055
Leaf area ($\log_{10}$)	−0.196	−0.831
SLA	−0.790	0.243
LDMC	0.701	−0.318
LNC	−0.676	−0.314
LPC	−0.765	0.035
Lδ^{13}C	0.469	−0.347

response groups (i.e. increasing, decreasing and stable species) along this component (Figure 5c and Figure S4). When a continuous rather than a discrete approach was followed, we found that the first component of the PCA explained 24% of the variance in population growth rate (Figure S5).

Three traits were significantly related to the elasticity of population growth rate to colonization: reproductive plant height, seed mass and leaf dry matter content (Figure 4b,h,p); these three relationships were negative, implying positive relationships with the elasticity of survival ($p < 0.01$ for all three relationships: data not shown). Relationships for the six remaining traits were not significant (Figure 4), as was the relationship with species scores on the first component of the PCA (Figure 5b). As a consequence of the second component of the PCA being driven by RPH and seed mass, the relationship between the elasticity of colonization and species scores on the second component of the PCA was significant ($r^2 = 0.22$, $p < 0.001$: Figure 5d).

4 | DISCUSSION

The underlying assumption of the present study is that differential changes in species abundances in response to management intensification reflect differences in ecological success related to contrasting functional and life-history strategies. Although this assertion can be considered as trivial, cross-species comparative analyses of the link between populations' demographic changes and plant functional traits, although one of the foundation stones of the discipline, remains scarce (Salguero-Gómez, Violle, Gimenez, & Childs, 2018; Shipley et al., 2016). This is partly due to the fact

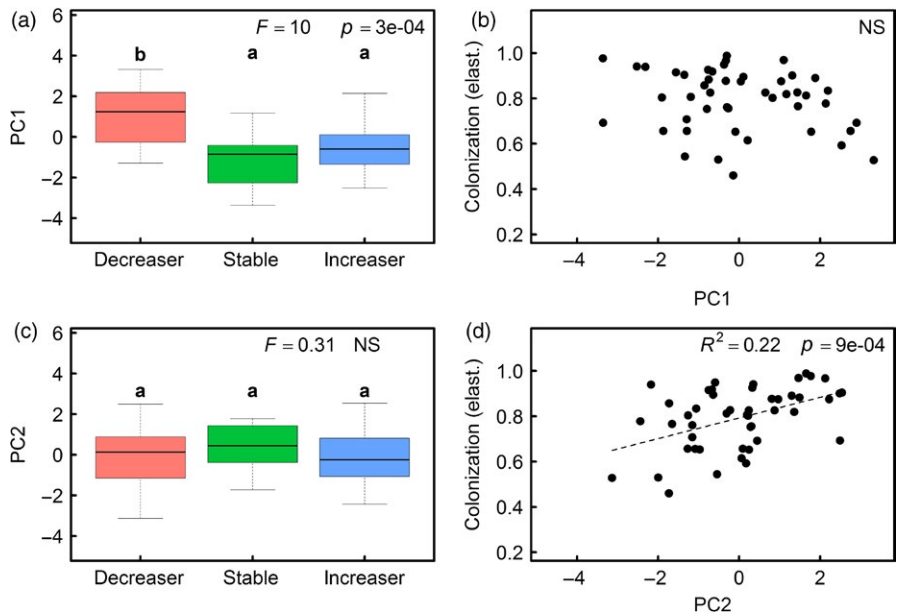

FIGURE 5 (a and c) Distributions of the scores on (a) the first (PC1) and (c) the second (PC2) components of a principal component analysis run on the nine traits listed in Table 1, for species from the three response groups identified on the basis of the values of changes in the probability of occurrence; more information on boxplots and meaning of letters and text can be found in the legend to Figure 3. (b and d) Relationships between the scores of species on (b) the first and (d) the second component of the PCA and the elasticity of colonization. Analogues of demographic parameters were calculated in the intensified management regime (G+F). The linear regression is not significant for PC1 (NS), while it is for PC2 (dashed line, R^2 and p values given on top of panel). Traits with the highest loadings on PC1 are (cf. Table 1): specific leaf area, leaf phosphorus concentration, leaf dry matter content and leaf nitrogen concentration; on PC2: leaf area, seed mass and reproductive plant height [Colour figure can be viewed at wileyonlinelibrary.com]

that tracking demographic changes of natural plant populations for multiple coexisting species simultaneously is challenging, both practically and methodologically. Here, we analysed long-term botanical surveys of plant communities, and used changes in plant cover over time to derive analogues of demographic parameters as an alternative to the standard individual-based assessment of vital rates (Caswell, 2001; Salguero-Gómez et al., 2015). We hypothesize that these parameters relate to changes in plant functioning induced by the modification of environmental conditions, that this functioning can be captured by key traits and axes of functional variation identified in plants (Grime, 1979; Westoby et al., 2002), and that these axes can be mapped onto components of life-history strategies (Salguero-Gómez et al., 2016).

4.1 | Vegetation response to intensified management

Temporal changes in the composition of vegetation over the 28-year period occurred in both management regimes, but were much stronger with increased fertilization and grazing pressure. The shift in community composition observed in the traditional regime in which the management practices were kept constant might be due to climatic changes: there was a 2.3°C increase of mean annual air temperature at the site over the 1978–2005 period with no significant trend in mean annual precipitation, resulting in an increased drought intensity likely to produce changes in community structure and composition. Interestingly, these changes in species composition did not lead to changes in the functional structure of communities (Chollet et al., 2014). These putative effects of changes in climate are likely to operate in the intensified management regime as well, but they cannot be sorted out from those of the management regime.

4.2 | Traits and demographic parameters

The temporal changes in the probabilities of species occurrence following management intensification in the G+F regime allowed us to classify species into decreasing, stable and increasing response groups. Compared to stable species and/or decreasers, increasers were characterized by a rapid life cycle (78% of annuals in the dataset were increasers, while all chamaephytes were decreasers), which is in line with the findings that short-lived, monocarpic species have a greater ability to respond to disturbances than perennial herbs and shrubs (Stott et al., 2010). Shorter life cycles can thus be interpreted as a response to increased grazing intensity in our study system. Increasers also have high values of leaf phosphorus concentration and low values of leaf dry matter content, and overall, they tended to flower between 1 and 2 weeks before decreasers and stable species (difference significant only with the latter group), which is commonly observed in response to grazing as well (see also Díaz et al., 2007; Garnier et al., 2007; Pakeman, 2004). Differences in these combinations of traits among response groups correspond to a shift in the position of species along the first component of the PCA. This component mostly differentiates decreasers from the two other groups, which are relatively close to one another in the phenotypic space defined by the PCA. This indicates that management intensification leads to the exclusion of species with high LDMC and low LPC (and low SLA to a lower extent), while species with opposite trait values either tolerate (stable species) or benefit from (increasers) the new conditions created by the high nutrient availability and grazing pressure. This combination of leaf traits broadly corresponds to the second axis of the global spectrum of plant form and function identified by Díaz et al. (2016), which can be interpreted as a fast-slow continuum of plant functioning (Reich, Walters, & Ellsworth, 1997; Shipley, Lechowicz, Wright, & Reich, 2006; Wright et al., 2004; see Garnier et al., 2016 for an overview): species with low rates of resource acquisition but efficient conservation of resources are progressively replaced by species with opposite characteristics, in relation with the intensification of management (cf. Garnier et al., 2016 and references therein). More generally, these changes in trait combinations correspond to the replacement of stress-tolerator by competitive/ruderal species as defined in Grime's (1979) ecological strategy scheme.

Changes in the probability of occurrences are expected to increase with the probability of colonization and decrease with the probability of mortality (Damgaard et al., 2017; Thuiller et al., 2014). We indeed found a positive, but weak, relationship between changes in the probability of occurrences and the elasticity of colonization, which is a measure of the relative importance of colonization for the change of population growth rate (assessed by changes in species cover in our study), compared to survival. The significant, negative, associations between the elasticity of colonization and both reproductive height and seed mass mean that these two traits have a negative impact on the plant colonization process. For reproductive height, this might be interpreted as a consequence of height having a positive effect on survival, which mechanically induces a negative effect on the importance of colonization. For seed mass, this might be due to the fact that this trait is expected to trade-off with seed number (Leishman, Wright, Moles, & Westoby, 2000; Shipley & Dion, 1992; Smith & Fretwell, 1974), and that seed number is likely to influence positively colonization/recruitment in the highly disturbed environment induced by the increased grazing intensity. The higher proportion of annuals is also indicative of an increased importance of recruitment as compared to survival in intensively managed communities (see also Franco & Silvertown, 2004). From a multivariate perspective, there was also a significant relationship between the elasticity of colonization and the second component of the PCA: this component is strongly structured by reproductive height and seed mass, broadly corresponding to the size axis of the global spectrum of plant form and function (Díaz et al., 2016).

Of the traits that differed among response groups, only one—leaf dry matter content—was also significantly related to colonization elasticity: species with low values of this trait have a higher probability to enter the community following the intensification of management than species with high values. LDMC therefore appears as a pivotal trait explaining the response of plants to an

increase in management intensity. LDMC, which informs on the density of tissues in leaves (cf. Garnier et al., 2016 and references therein), has been assumed to be a central underlying trait driving the fast-slow ecophysiological continuum (Shipley et al., 2006; discussed in Mason, Goolsby, Humphreys, & Donovan, 2016), and was found to be a better predictor of both soil fertility (Hodgson et al., 2011) and above-ground net productivity in temperate ecosystems (Smart et al., 2017) than specific leaf area. Our study further confirms these findings, and shows that low LDMC species that acquire resource rapidly are more likely to enter the communities and outcompete high LDMC species in conditions of high resource and/or high disturbance.

4.3 | Connecting trait and life-history frameworks

Altogether, our results show that the combination of traits used to describe the phenotype explains 22%–24% of the variance of major demographic parameters of populations following management intensification. These findings offer prospects to connect trait-based and demographic approaches to plant functioning, in the context of the frameworks recently proposed by Díaz et al. (2016) on the one hand, and Salguero-Gómez et al. (2016) on the other hand. The intensification of management led to the replacement of "slow" by "fast" species (cf. Wright et al., 2004) along the first axis of the global spectrum of plant form and function (Díaz et al., 2016), which echoes the first axis of the plant life-history ordination: the contrasting responses of annuals, which were mostly increasers, and chamaephytes, which were all decreasers, suggest in particular that increased fertilization and grazing pressure selects for species with short generation time and early age at maturity (we do not have information on these variables for herbaceous perennials).

Interestingly, we found that the relative contribution of colonization to population change was not associated with the fast-slow continuum of leaf functioning, but with the organ size axis (plant height, seed mass) of the global spectrum of plant form and function. This corroborates only partially Adler et al.'s (2014) results who showed significant relationships between specific leaf area and elasticities of population growth rate to growth, fecundity and survival across 222 species distributed world-wide, and a positive relationship between seed mass and elasticity of population growth rate to survival (which was also found here: $r^2 = 0.37$, $p < 0.01$; data not shown). If we assume that seed size is indicative of the quantity of seeds produced *per* square metre of canopy cover (discussed in Henery & Westoby, 2001; Moles, Falster, Leishman, & Westoby, 2004), we may tentatively connect this trait to net reproductive rate, one of reproductive features contributing most to the second dimension of life-history strategies as identified by Salguero-Gómez et al. (2016).

However, a number of limitations to the generality of this coupling between trait and life-history dimensions have to be put forward. First, variations in a given environmental factor might induce changes in demographic parameters, which may strongly contribute to the fast-slow continuum of life histories such as longevity or progressive or retrogressive growth (Salguero-Gómez, 2017) without inducing changes in species positions along the fast-slow continuum of plant functioning. In our study system for example, leaf dry matter content, the trait found to be best connected to demographic parameters, does not vary significantly between the two management regimes for most species (Figure S6). This is the case in particular for *Carthamus mitissimus* and *Galium corrudifolium*, whose abundance decreased with time in the intensified regime, while their abundance did not change significantly over the 1978–2005 period in the traditional regime (results not shown). This implies that the relationship between leaf dry matter content and species demographic parameters is likely to depend on the environmental conditions under which it is established. This specific example points to the need of considering intraspecific variation in both functional traits and demographic parameters simultaneously, an area of research which would prove particularly valuable in the future.

Second, there are cases in which a given trait responds differently to changes in a specific environmental factor: compare for example the contrasting responses of specific leaf area to temperature in, e.g. Wright et al. (2005), Moles et al. (2014), Read, Moorhead, Swenson, Bailey, and Sanders (2014) and Simpson, Richardson, and Laughlin (2016). The variations of this trait might therefore not be interpreted as adaptive in all situations (see also Lajoie & Vellend, 2015). This highlights that traits which are considered "functional," i.e. which relate to fitness components (McGill et al., 2006; Violle et al., 2007), might sometimes be only poorly related to demographic processes, and hence to ecological success (Ackerly & Monson, 2003; Shipley et al., 2016). Two directions can be proposed to overcome this difficulty: (i) using traits more closely related to the mechanism underlying plant response to specific environmental factors (cf. Chapin, Autumn, & Pugnaire, 1993), which implies that the relationships between traits and demographic/life-history parameters will be context-dependent and (ii) accounting for a higher number of axes of functional variation. Here we focused mainly on traits related to the fast-slow continuum on the one hand and to the size/reproductive dimension on the other, but there is evidence that considering a broader range of trait combinations corresponding to other aspects of plant functioning is essential to understand properly the matching between organisms and their environment (Kleyer & Minden, 2015; Laughlin, 2014; Laughlin & Messier, 2015).

Linking traits and demography is a necessary step to advance the field, both theoretically and predictively (Enquist et al., 2015; Salguero-Gómez et al., 2018). Here we show that a combination of traits widely used in plant functional ecology to describe phenotypes relates significantly to vital rates of populations, but we also argue that accounting for the local environmental context is essential to establish robust and predictable relationships between traits and demographic parameters.

5 | CONCLUSIONS

Our study is an attempt to conciliate trait-based and demographic approaches to plant functioning, two streams of research that have

developed somewhat independently. We show that traits capturing the fast-slow continuum of plant functioning relates to plant species demographic response to management and to several components of the fast-slow continuum of life histories. The elasticities of population growth rate to colonization and survival are related to the organ size axis of the global spectrum of plant form and function, and to net reproductive rate, one of the major features of the reproductive dimension structuring life-history strategies. These results therefore show that some of the traits most widely used to describe the functional space of plants can, to some extent, be related to important aspects of their demography. However, whether relationships will remain consistent and whether the small set of traits currently used will be relevant to all situations is questionable. Improving the connection between functional and life-history approaches to plant ecology will require not only a more detailed description of the phenotype involving a higher number of functional dimensions but also a better assessment of environmental conditions under which both functional traits and life-history components are assessed.

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AUTHOR'S CONTRIBUTIONS

E.G., A.F., M.-L.N., P.C. and C.V. conceived the ideas and designed methodology. P.A. ran the field site and coordinated experiments. E.G., A.F., M.-L. N., P.C., D.H. and J.R. collected the data. E.G., A.F., C.D., C.L. and C.V. analysed the data. E.G. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data are available from the Dryad Digital Repository https://doi.org/10.5061/dryad.8463q13 (Garnier et al., 2018).

ORCID

Eric Garnier http://orcid.org/0000-0002-9392-5154

Cyrille Violle http://orcid.org/0000-0002-2471-9226

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SUPPORTING INFORMATION

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